The eyes and ears are visual indicators of attention in domestic horses

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evolutionary theory. We do not know if the early animal ancestors really looked like worms. But systematic molecular analyses in *Platynereis* and even more distantly related animals, such as sea anemones, indeed suggest that these worms share more similarities with the early animal ancestors than, for instance, a fruit fly does. A prime example is the so-called ciliary photoreceptor cells that were uncovered in the *Platynereis* brain and correlate much better with the light receptors in the human retina than with the photoreceptors of insect eyes. Facts like these facilitate comparisons to vertebrate model systems, and thereby have contributed to the success of *Platynereis* as an important reference species for comparative and evolutionary developmental biology (evo-devo).

So do these worms allow us to study the brain of the past? *Platynereis* has of course been shaped by hundreds of millions of years of evolution. No one would therefore assume that the brain has remained unchanged over this time span. But in order to reconstruct such an early brain, it is very useful to have access to invertebrates, such as *Platynereis,* in which a larger part of the original set of cell types, such as the ciliary photoreceptors, have been retained, rather than lost. As the animals are translucent, live imaging and manipulation of neurons are possible, and new results in larvae show that neuronal circuits can be experimentally dissected.

With their many segments and legs, these worms look like millipedes. Is there any connection? Segmentation is another area in which *Platynereis* provides interesting insights. For a long time, scientists grouped annelids like *Platynereis* together with millipedes and other arthropods into one clade of segmented animals. But like the unsegmented nematodes mentioned before, millipedes are part of the ecdysozoan superphylum. Hence, a big question is whether or not the ancestor of all these animals already possessed segments. Molecular research into *Platynereis* segmentation has revealed similar patterning molecules to those used in insect segment formation, therefore this is a fruitful direction to study. Moreover, young worms have the ability to regrow large parts of their trunk after injury. How do the mechanisms responsible relate to the processes in other regenerating animals, such as *Hydra*, planarians or salamanders? There are many such questions in which a strong annelid model system can help to advance our understanding of nature.

Interesting biology, but how about suitable tools to study it? The molecular and behavioural toolbox available for this species ranges from behavioural studies on swimming larvae and adult worms to sophisticated genetic manipulations, such as targeted mutagenesis, stable transgenesis, and conditional cell ablation. As each mating results in hundreds of synchronously developing embryos, it is possible to perform systematic analyses on gene expression at different time points of development with cellular resolution. Unlike many other marine model species, *Platynereis* is easily reared in inland laboratories at low cost, feeding on home-grown algae, organic spinach and pet fish food. In fact, the major wild-type strains in use today have been continuously bred for more than 60 years in captivity. Several highly inbred strains, as well as an increasing number of stable transgenic and mutant strains, are available. So, there are plenty of resources and tools to tackle fresh biological questions in this species.

Where can I find out more?

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The eyes and ears are visual indicators of attention in domestic horses

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Sensitivity to the attentional states of others has adaptive advantages [1], and in social animals, attending to others is important for predator detection, as well as a pre-requisite for normal social functioning and more complex socio-cognitive abilities [2]. Despite widespread interest in how social species perceive attention in others, studies of non-human animals have been inconclusive about the detailed cues involved [3]. Previous work has focused on head and eye direction, overlooking the fact that many mammals have obvious and mobile ears that could act as a visual cue to attention. Here we report that horses use the head orientation of a conspecific to locate food, but that this ability is disrupted when parts of the face (the eyes and ears) are covered up with naturalistic masks. The ability to correctly judge attention also interacted with the identity of the model horse, suggesting that individual differences in facial features may influence the salience of cues. Our results indicate that a combination of head orientation with facial expression, specifically involving both the eyes and ears, is necessary for communicating social attention. These findings emphasise that in order to understand how attention is communicated in non-human animals, it is essential to consider a broad range of cues.

Studies using naturalistic gaze-following paradigms have indicated that a wide range of animals, from crows to chimpanzees, follow the attention of conspecifics [2]. However, gaze is often used as a general term encompassing head orientation, eye direction and any other potential indicators. Consequently, it is difficult to establish exactly what cues are informative, and previous experimental work exploring this has focused on cues that humans use, in particular, head orientation and eye gaze [3,4], potentially overlooking

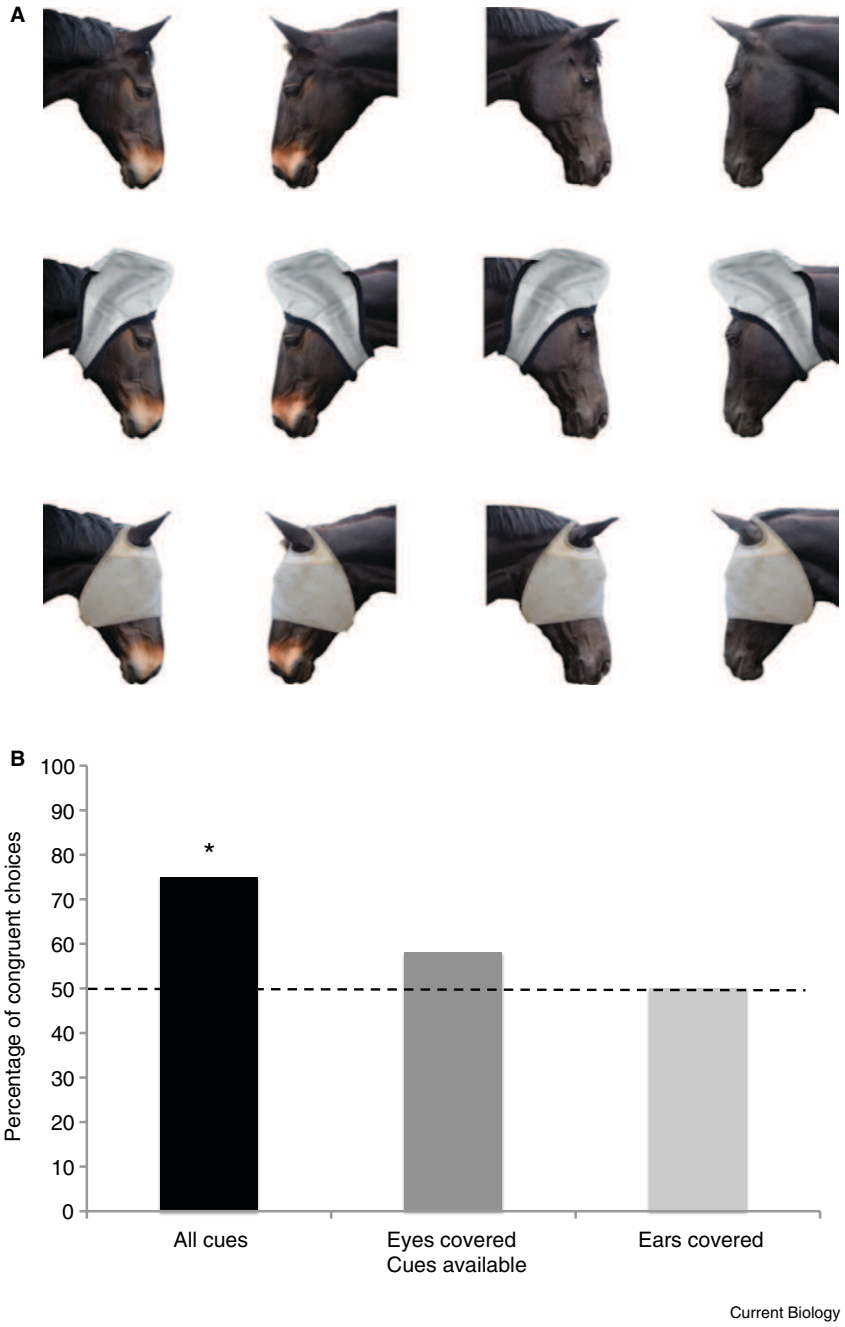

Figure 1. Illustration of stimuli and main results.
(A) Photographic stimuli including manipulations that incorporate fly masks to cover key internal features of the face. The photographs were reproduced at life size and used as the model in an object choice task to establish whether horses could use the head orientation and facial expression of a conspecific to locate hidden food. Both model horses are shown here in the three experimental conditions: all cues visible; ears covered; eyes covered. WG is the horse on the left of the image; MC is the horse on the right. (B) Percentage of horses choosing the congruent bucket for each condition. Asterisk: P < 0.05 (binomial probabilities, two tailed).

a wealth of other available information. Animals with a different facial morphology — particularly those with large, mobile ears — may have other means of signaling.

Horses are a prey animal with advanced social relationships [5–7], and within the domestic environment they often have parts of their faces covered by riding equipment or masks used for protection from flies. We used these masks, presented within photographic stimuli, to investigate whether horses were responsive to the attentional cues of another horse, and if so what areas of the face were important in providing information (Figure 1A, Supplemental Information and Figure S1).

In our experiment, horses were clearly sensitive to the attentional state of a conspecific and this influenced their decision about where to feed. When subjects viewed the unoccluded image of another horse looking at one of two buckets containing food, they were more likely to feed from the bucket congruent with the model (n = 24, K = 18, P = 0.02; Figure 1B). However, when either the eyes or ears were covered the choices of the participants dropped to chance levels (eyes: n = 24, K = 14, P = 0.54; ears: n = 24, K = 12, P = 1), suggesting these were both key areas informing the participants' decisions.

The cues available — whole head visible, eyes covered, or ears covered — also influenced the time spent looking at the photographs ($F(2,62)$ = 3.62, P = 0.03; see also the Supplemental Information). Planned comparisons revealed that horses looked for significantly longer when all the information was visible, compared to when the ears or the eyes were covered (P < 0.01). However, there was no difference in looking time when the ears were covered compared to when the eyes were covered, nor was looking time influenced by the identity of the model horse.

Additionally, more subtle effects were also apparent. Cues available, age, sex, testing centre, model horse viewed, and stimuli direction were entered as predictors in a logistic regression with feeding choice as the response variable (0 = choice incongruent with model; 1 = choice congruent with model; Supplemental Information and Table S1). This revealed a significant interaction, whereby sensitivity to the cues available differed according to the model horse viewed. Covering the eyes (Figure 1A) had less influence on subjects that viewed model MC than subjects who viewed model WG (see also Supplemental Information), potentially indicating that differences in the facial features or expression of the two models affected the salience of cues, and highlighting an interesting area for future research.

We also conducted additional presentations of single images as controls to verify that covering key parts of the face did not impede subjects' recognition of the stimuli as depicting a horse. When subjects

were allowed to view our horse stimuli at close range they showed similar reactions to all three conditions (all cues visible, eyes covered, ears covered), which were significantly different from their responses to appropriately matched control stimuli (phase-scrambled counterparts of the originals; Supplemental Information). Furthermore, subjects were more likely to approach the original stimuli and more likely to avoid the controls, as would be predicted if they were responding to photographs of horses versus novel objects (see details in Supplemental Information). We also took precautions to avoid the possibility of a 'Clever Hans Effect' occurring through incidental cueing by the experimenter. In particular, the experimenter was unfamiliar to the horse, kept ignorant of which stimuli would be presented and, cruicially, after the release point (when the choice was made) they stood facing away from the horse, so could not see the horse's choice or provide any feedback (full details in Supplemental Information).

Our results provide the first evidence from an animal with laterally placed eyes that cues from this area convey important information. Eye gaze is difficult to isolate in animals with eyes positioned at an oblique angle, and it had been suggested that non-primates cannot use eye gaze independently of head orientation [2,4]. However, we demonstrate that the eyes do carry information, even when laterally placed in an animal far removed from the primate lineage. Horses, along with other ungulates, have a white sclera that is visible in various situations [6]. This plus other cues, such as dilation of the pupil and movement of the facial muscles surrounding the eye, could be informative of attentional state, as they are in humans [8].

Most significantly, our results demonstrate that animals with large, mobile ears can use these as a visual cue to attention. While anecdotal accounts of this exist in the literature (for example [6]) the potential role of the ears in signaling has been overlooked in previous experiments. In animals that have evolved a differently shaped face it is important to consider cues that humans do not have, and novel paradigms that incorporate these will be crucial in developing a full understanding of attentional mechanisms across species.

Supplemental Information
Supplemental Information includes experimental procedures, supplemental results, one figure, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.06.023.

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Influence of prior information on pain involves biased perceptual decision-making

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Prior information about features of a stimulus is a strong modulator of perception. For instance, the prospect of more intense pain leads to an increased perception of pain, whereas the expectation of analgesia reduces pain, as shown in placebo analgesia and expectancy modulations during drug administration [1]. This influence is commonly assumed to be rooted in altered sensory processing and expectancy-related modulations in the spinal cord [2], are often taken as evidence for this notion. Contemporary models of perception, however, suggest that prior information can also modulate perception by biasing perceptual decision-making — the inferential process underlying perception in which prior information is used to interpret sensory information. In this type of bias, the information is already present in the system before the stimulus is observed [3]. Computational models can distinguish between changes in sensory processing and altered decision-making as they result in different response times for incorrect choices in a perceptual decision-making task (Figure S1A,B) [4]. Using a drift-diffusion model, we investigated the influence of both processes in two independent experiments. The results of both experiments strongly suggest that these changes in pain perception are predominantly based on altered perceptual decision-making.

Thirty-four right-handed healthy volunteers (23 female; mean age 23.4 years) took part in the study in Experiment 1. In a probabilistic cueing paradigm, participants were presented with one of two visual cues in each trial. Cue 1 signaled the subsequent application of a high intensity noxious electrical stimulus with a probability of 80% and of a low intensity stimulus with a probability of 20%. Cue 2